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LINKAGE IN LYCOPERSICUM

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THE known cases of linkage of hereditary factors in plants are not as yet so numerous but that it seems desirable to place on record all instances of this condition. With that end in view I wish to call attention to some scattered data obtained several years ago, before much was known about linkage, and presented in publications which are probably not widely circulated.

Part of the data to be considered resulted from an investigation, started by Hedrick and Booth, shortly after the beginning of the awakened interest in Mendelism, which was designed to test the inheritance of Mendelian characters in the garden tomato (*Lycopersicum esculentum* Mill.). The results were published in the *Proceedings* of the Society for Horticultural Science in 1907. Two different crosses were studied. One cross was made between two varieties which differed in one character only, viz., standard and dwarf habit of vine. The other cross was between two varieties which differed in three characters, habit of vine, shape of fruit and color of fruit. It is this second cross which gives evidence that there is a genetic linkage between the factors for habit of vine and shape of fruit.

In this latter cross the varieties used are known under the varietal names of Quarter Century and Yellow Pear. The Quarter Century variety is described as having a dwarf type of vine, red-colored fruit which is shaped like that of the common garden varieties, *i. e.*, more or less spherical. The Yellow Pear variety has a standard or spreading vine, fruit yellow in color and pear-shaped.

The first generation plants grown from this cross were standard in habit of vine, with red-colored fruit which differed in shape from either parent, being oval rather

⁴ Parental combinations.

From the results as given it can be seen that the plants with the combinations of habit of vine and shape of fruit obtained in F_2 which duplicated the parental combinations, are more numerous than expected, whereas the two new combinations, with respect to these two factors, are less than expected. The writers observed these facts and commented upon them as follows:

The percentage of plants which fall into each class are, however, quite different from those of Mendel. This is of importance in that it indicates the number of plants which it is necessary to grow in order to get a plant with a certain combination of characters. Theoretically, 64 plants should have included all the combinations we secured; actually, with 452 plants there is one combination with only one representative. In place of one representative, there should have been seven. Our results would indicate that it is necessary to raise seven times as many tomatoes as are theoretically necessary in order to secure a desired combination. There is apparently a method to this variation. *The tendency seems to be for the second generation hybrids to go back to the same combinations of characters as the parents, rather than to form new ones.*¹ Thus it will be seen that the tomato with Quarter Century fruit on Yellow Pear vines is less than theoretical considerations alone would indicate, while the number of tomatoes with Quarter Century fruit on Quarter Century vines is more than theory would require; the same being true for the yellow pear. Inertia seems to be a factor and the preservation of the *status quo* an object among tomatoes as among men (p. 23).

In the light of more recent investigations of factorial linkage it is recognized at once that the above statement fulfils the conditions of linkage between at least two of the allelomorphic pairs concerned. Let us then examine the data more closely to see if a clear case of linkage can be made out.

Since the deviations above and below the expectancies are about the same in both the red-fruited and yellow-fruited plants, it indicates that color of fruit is an independent factor and that habit of vine and shape of fruit are partially linked with frequent breaks in the linkage. Combining the figures for yellow and red fruit and putting the 452 plants into 6 categories instead of 12, the condensed results given in Table II are obtained.

¹ The italics are mine.

TABLE II

DISTRIBUTION OF THE F_2 PLANTS WITH RESPECT TO THEIR HABIT OF VINE
AND SHAPE OF FRUIT

Categories	Found	Expected	Found	Expected	Combinations of Characters
Standard vine, spherical fruit	61	$84\frac{3}{4}$	} 379	339	New combination
F ₁ fruit.....	188	$169\frac{3}{4}$			Parental combination
Pear-shaped fruit.....	127	$84\frac{3}{4}$			
Dwarf vine, spherical fruit.....	50	$28\frac{1}{4}$	} 73	113	Parental combination
F ₁ fruit.....	20	$56\frac{1}{2}$			New combination
Pear-shaped fruit.....	3	$28\frac{1}{4}$			
Total.....	452	452	452	452	*

These figures bring out more clearly the fact that the parental combinations are in excess while the new combinations are deficient when compared with the theoretical expectations with independent assortment. Combining the numbers of the three types of standard plants and the three of dwarfs brings out another fact, viz.: that the standards exceed the dwarfs far more than is to be expected. This result can not be accounted for on the basis of linkage, because it makes no difference whether habit of vine is or is not linked with any other factor; the ratio of the total number of standards to the total number of dwarfs should approach a ratio of 3:1, if the two characters form a simple allelomorphic pair free from any other complicating factors. The same deficiency of dwarfs was noted by these investigators in the other cross reported in both the F_2 generation and the F_3 generation from heterozygous F_2 plants. The numbers they obtained were as follows:

	Found	Expected
Stone \times Dwarf Aristocrat, F_2 : Standards	2,289	2,176
Dwarfs	612	725
Stone \times Dwarf Aristocrat, F_3 : Standards	1,086	1,026
Dwarfs	282	342

With regard to this deficiency of dwarfs Hedrick and Booth suggest that

the smaller number may be due to a lesser vigor on the part of the dwarf as compared with the standard plants, and an unconscious selec-

tion by the man pricking out the young plants from the seed boxes, of the larger, that is, the standard plants. This point had been anticipated and the workmen cautioned to take the plants just as they came, but it is against all of a gardener's training to throw aside a good vigorous plant and take one half the size.

However, in the F_3 plants given above, from F_2 segregating plants, all the seeds which were planted and lived were grown to maturity, so that the latter source of error, of unequal sampling, was avoided. Still there was the same deficiency of dwarfs.

Craig (1907), in the same publication, reports large numbers of the same cross which also showed a deviation in the second generation, of too many standard plants. He does not state whether or not an attempt was made to grow all the plants obtained from the seed planted. His figures are as follows:

	Found	Expected
Stone \times Dwarf Aristocrat, F_2 : Standards . . .	2,499	2,367
Dwarfs	657	789
Stone \times Dwarf Aristocrat, F_3 : Standards . . .	154	155
Dwarfs	52	51

Both Halsted (1905) and Price and Drinkard (1908) give figures on the proportions of standard and dwarf plants obtained in F_2 populations. I have tabulated their data as follows:

Halsted's Data (pp. 450-462)

	Standards	Dwarfs
Dwarf Champion \times Magnus, F_2	65	20
Dwarf Stone \times Golden Queen, F_2	25	5
Dwarf Stone \times Extra Early Tree, F_2	14	6
Lemon Blush \times Dwarf Champion, F_2	18	3
Total found	122	34
Expected	117	39

Price and Drinkard's Data (Table XI, p. 40)

	Standard	Dwarf
Dwarf Champion \times Red Currant	21	3
Potato Leaf \times Dwarf Champion	15	9
Total found	36	12
Expected	36	12

In these last two tabulations many of the crosses show a deficiency of dwarfs, although the results as a whole agree closely with expectations. However, the numbers are too small to place much weight upon.

In connection with another investigation I have obtained considerable data on the inheritance of this character, by simply growing the seedlings in flats from 6 to 8 weeks, and then counting the dwarfs and standards without setting the plants in the field, as in all the previous cases cited. It is not always possible to distinguish all of the two types of plants, with certainty, at this stage especially, if the plants are crowded and there are many small stunted plants. However, counting the plants at this time removes the possibility of unequal sampling when only a part of the seedlings are set in the field, and also the possibility of differential viability in the field. The distributions in 5 F_2 and 16 F_3 populations from heterozygous F_2 plants gave the following results:

	Standards	Dwarfs
Dwarf Champion \times Stone, 5 F_2 populations	1,103	437
Dwarf Champion \times Earliana, 1 F_2 population ...	186	67
Dwarf Champion \times Stone, 12 F_3 populations ..	1,707	730
Dwarf Champion \times Earliana, 4 F_3 populations ..	571	149
Total found	3,567	1,383
Expected	3,713	1,237

Here the deviation from expectation is in the opposite direction. There is an excess of dwarfs. It would seem that too many of the small plants were classified as dwarfs when they were really standards. Two of the above F_2 populations were grown longer than the others in flats which were not so crowded, so that the errors in classification, I believe, were more nearly overcome. The following results were obtained:

	Standards	Dwarfs
Dwarf Champion \times Stone, F_2	268	88
Dwarf Champion \times Earliana, F_2	186	67
Total found	454	155
Expected	457	152

From these data it seems justifiable to conclude that dwarfness and standardness form a simple allelomorphic pair, free from any genetically complicating factors.

I have gone to this length to demonstrate the normal behavior of this character in order to be able to correct Hedrick and Booth's data according to the proportion of dwarf and standard plants, which presumably they should have obtained if all the plants had been grown to maturity, and if there had been equal viability. Moreover, whether or not the deficiency of dwarfs which they obtained is due to unequal sampling, differential viability or some unknown cause, there is no reason to suppose that the cause, whatever it is, has anything to do with the linkage between the factors for habit of vine and shape of fruit. I have, therefore, in Table III increased the num-

TABLE III

CORRECTED DISTRIBUTION OF THE F_2 PLANTS WITH RESPECT TO THEIR HABIT OF VINE AND SHAPE OF FRUIT—CHARACTERS WHICH SHOW LINKAGE

Genetic Formulae	Characters of F_2 Plants	1. Found	2. Expected	3. Corrected	4. Expected	Combinations of Characters
AB....	Standard vine, non-constricted fruit	252	254	252	284	New combination
Ab.....	Standard vine, constricted fruit.....	127	85	127	95	Parental combination
aB.....	Dwarf vine, non-constricted fruit...	70	85	121	95	Parental combination
ab.....	Dwarf vine, constricted fruit.....	3	28	5	31	New combination
Total.. .. .		452	452	505	505	

ber of dwarfs to the number theoretically expected, keeping the proportion of the two different kinds of dwarfs the same with respect to shape of fruit. From Table II it can be noted that 379 standards were obtained. Theoretically the dwarfs should have been one third of this number, or 126.3. There were actually only 73. This number would have to be increased 1.73 times in order to bring the number of dwarfs up to the expected number. Combining both the standard and dwarf plants in two classes each, those with and those without constricted fruit, and multiplying these two classes of dwarf plants

by 1.73, the figures given in column 3 of Table III are obtained. The figures in this column represent the number of plants which presumably should have been obtained in the four different categories, if the expected number of dwarf plants had been obtained.

These corrected numbers can then be compared with the closest theoretical ratio where the gametes, instead of being produced in the equal proportion of 1 AB:1 Ab:1 aB:1 ab, were produced in unequal proportions (where A and B represent the two dominant factors—standard vine and non-constricted fruit). In this case if the gametes were formed in the proportion of 1 AB:4 Ab:4 aB:1 ab, the agreement between the corrected result and the theoretical expectation is surprisingly close.

	AB : Ab : aB : ab
Corrected numbers	252 : 127 : 121 : 5
Corrected ratio	50.4 : 25.4 : 24.2 : 1
Theoretical ratio	51 : 24 : 24 : 1
(1:4:4:1 gametic series)	

It is seen that the data obtained by Hedrick and Booth give a clear indication of linkage of the factor for standard vine with that for constricted fruit and dwarf vine with non-constricted fruit. Frequent breaks in the linkage occur to form the two new combinations. On the chromosome hypothesis the data show, in this case, that crossing over occurs in 20 per cent. of the gametes formed.

TABLE IV

CORRECTED DISTRIBUTION OF THE F₂ PLANTS WITH RESPECT TO THEIR HABIT OF VINE AND COLOR OF FRUIT—CHARACTERS WHICH DO NOT SHOW LINKAGE

Genetic Formule	Characters of F ₂ Plants	1. Found	2. Expected	3. Corrected	4. Expected	Combinations of Characters
AB....	Standard vine, red fruit.....	294	254	294	284	New combination
Ab....	Standard vine, yellow fruit.....	85	85	85	95	Parental combination
aB....	Dwarf vine, red fruit.....	56	85	97	95	Parental combination
ab....	Dwarf vine, yellow fruit.....	17	28	29	31	New combination
	Total.....	452	452	505	505	

The data also show that there is no linkage between the other two combinations of factors reported, viz., vine habit and fruit color, and fruit color and fruit shape. Correcting the number of dwarfs in the same way as in Table III the results for these two combinations of factors are given in Tables IV and V.

TABLE V

CORRECTED² DISTRIBUTION OF THE F₂ PLANTS WITH RESPECT TO THEIR SHAPE OF FRUIT AND COLOR OF FRUIT—CHARACTERS WHICH DO NOT SHOW LINKAGE

Genetic Formula	Characters of F ₂ Plants	1. Found	2. Expected	3. Corrected	4. Expected	Combinations of Characters
AB....	Non-constricted, red fruit	250	254	289	284	Parental combination
Ab....	Non-constricted, yellow fruit.....	72	85	84	95	New combination
aB....	Constricted, red fruit	100	85	101	95	New combination
ab....	Constricted, yellow fruit.....	30	28	31	31	Parental combination
	Total.....	452	452	505	505	

From these two tabulations it will be seen that the agreement between expectation and observation, when the number of dwarfs is increased to the number expected, is reasonably close, and the deviation from the expected is not such as to suggest linkage between any of these factors.

Both Halsted, and Price and Drinkard, in the publications previously mentioned, give a large number of crosses of tomatoes where the inheritance of many different characters are studied. Unfortunately, in most cases the data are presented in such a way as to show the inheritance of only one character pair at a time.

Halsted gives a dihybrid cross between two varieties differing in habit of vine—standard (A) and dwarf (a), and margin of leaf—serrate (B) and entire (b). The

² Since habit of vine is not concerned in this cross it is, of course, unnecessary to correct for the low number of dwarfs as in the two previous tables. I have done so simply to show that it does not affect the goodness of fit to any great extent.

cross was made in such a way that one dominant factor entered from each parent. The numbers obtained

	AB: Ab: aB: ab
Found	49: 16: 13: 7
Expected	48: 16: 16: 5

do not indicate any linkage between these factors.

Price and Drinkard's data indicate that there is no linkage between shape of fruit and color of fruit in two different crosses (agreeing with the data given in Table V), none between foliage color and fruit color, and none between foliage color and fruit shape. In these crosses the numbers are too small to be sure of the conclusions with regard to linkage. They give the results of a cross, however, which shows complete linkage between green foliage color and two-celled fruit, as opposed to yellow foliage color and many-celled fruit. Only 24 F₂ plants were grown, which were of two types only, duplicating the parents.

These characters, foliage color and loculation of ovary, can not be the expression of the same factor because many varieties are known with these characters combined in the other ways. In fact the majority of the common garden varieties have green foliage and many-celled fruit. Neither does it seem probable that these dissimilar characters form a series of multiple allelomorphs as some cases of complete linkage, for instance, cob and pericarp colors in maize, are considered to be. Although the number of plants is small, as the writers state, it would seem that among 24 plants at least one new combination would appear if the factors were independent of each other. Larger numbers of a similar cross, studied by back crosses in the more favorable way, will probably show these factors to be partially linked.

Crane (1915) reports a cross between varieties of tomatoes differing in rather complex characters of inflorescence and fruit shape. He obtained figures which indicate partial linkage in these characters, but states that "the

numbers are not sufficiently large to form any conclusion as to the intensity of the coupling, nor to establish the existence of the same with certainty."

A number of clearly segregating characters are known in the tomato. Halsted lists 7 alternative unit character pairs, while Price and Drinkard give 13. However, from their own statements in regard to the behavior of these characters, and from my own rather limited experience with tomatoes, the number of different character pairs which they list should be reduced. For instance, only two allelomorphic pairs are known for color of fruit, viz., red and yellow flesh or endocarp, and yellow and colorless fruit skin or epicarp; while Price and Drinkard give four, and Halsted three, character pairs of fruit color. Different combinations of skin colors and flesh colors give the different colored fruits. For example, colorless epicarp over red endocarp gives pink-colored fruit.

TABLE VI

MENDELIAN CHARACTERS IN THE GARDEN TOMATO

(Revised from the lists given by Halsted and by Price and Drinkard.)

		Dominant	Recessive
Fruit shape.....	1	Spherical (non-constricted).....	Pyriform (constricted)
Fruit shape.....	2	Roundish conic.....	Roundish compressed..
Loculation of ovary.....	3	Bilocular.....	Plurilocular.....
Endocarp color.....	4	Red	Yellow.....
Epicarp color.....	5	Yellow.....	Colorless.....
Fruit surface.....	6	Smooth.....	Pubescent.....
Vine habit and leaf surface.....	7	{ Standard.....	{ Dwarf.....
Leaf margin.....	8	{ Smooth.....	{ Rugose.....
Leaf type.....	9	Serrate (normal or fine leaf).....	Entire ("potato" or coarse leaf).....
Foliage color.....	10	<i>Pimpinellifolium</i> type...	<i>Esculentum</i> type.....
Inflorescence type ³	11	Green.....	Yellow.....
		Simple.....	Compound.....

It is somewhat uncertain as to the number of independent factors concerned in fruit shape. According to Crane (*loc. cit.*) and Groth (1912 and 1915) there are a number of factors and it is not always possible to distinguish between the various shapes. There is apparently a corre-

³ See Crane, 1915, p. 4.

lation between the loculation of the ovary and some fruit shapes, although not necessarily with the constricted type of fruit. The foliage characters (Groth, 1911) are rather complicated. Also the color of foliage and the color of the epicarp of the fruit may be associated in the same way that habit of vine and leaf surface are, *i. e.*, the expressions of one factor. Dwarf plants always have a more rugose foliage than standard plants. According to Groth (1915, p. 17) dwarfness can not be associated with pubescent fruit for some reason.

A list of the Mendelian genes, so far known in the tomato, is given in Table VI.

The list is only tentative. A more detailed study of these characters will probably necessitate further revision. Other character differences may be known and should be added. There are, however, at least 10 plainly segregating genes and probably more. The behavior of 6 of these with respect to their being linked or not linked with each other, in all the 15 possible combinations,⁴ is known in the case of 7 of them and can be predicted for 5 others. These 15 combinations with respect to linkage are summarized as follows:

CHARACTERS SHOWN TO BE LINKED FROM THE DATA OF HEDRICK AND BOOTH,
AND PRICE AND DRINKARD

Vine Habit,	7	with	Fruit Shape,	1
Foliage Color,	10	with	Loculation of Ovary,	3

CHARACTERS SHOWN NOT TO BE LINKED FROM THE DATA OF HEDRICK AND
BOOTH, HALSTED, AND PRICE AND DRINKARD

Vine Habit,	7	with	Endocarp Color,	4
Vine Habit,	7	with	Leaf Margin,	8
Fruit Shape,	1	with	Endocarp Color,	4
Fruit Shape,	1	with	Foliage Color,	10
Endocarp Color,	4	with	Foliage Color,	10

⁴ The possible number of combinations is obtained from the formula $\frac{n^2 - n}{2}$ where n^2 equals the total number of combinations, two at a time, between n different units but no factor can, of course, be paired with itself and the remaining pairs are duplicated.

CHARACTERS WHICH CAN NOT BE LINKED (ON THE CHROMOSOME HYPOTHESIS
IF THE ABOVE CASES HOLD TRUE)

Endocarp Color,	4	with	Loculation of Ovary,	3
Vine Habit,	7	with	Loculation of Ovary,	3
Vine Habit,	7	with	Foliage Color,	10
Fruit Shape,	1	with	Leaf Margin,	8
Fruit Shape,	1	with	Loculation of Ovary,	3

CHARACTERS WHICH MAY OR MAY NOT BE LINKED

Leaf Margin,	8	with	Loculation of Ovary,	3
Leaf Margin,	8	with	Endocarp Color,	4
Leaf Margin,	8	with	Foliage Color,	10

Since not all the possible combinations of the 6 factors have been tested, and 4 of the factors have not been tested at all, either in combinations among themselves or with any of the other 6 factors, the possibilities of linkage in the tomato have only begun to be examined. It is noteworthy that none of the 7 combinations which either do or do not show linkage are at variance with the interpretation of linkage according to the chromosome hypothesis. For instance, where one of two linked genes is unlinked with a third, the other linked gene is also unlinked with it. This is a necessity on the chromosome hypothesis.⁵

To fit the facts to the chromosome hypothesis it is only necessary to assume that genes 1 and 7 are located in one chromosome which we may call A; genes 3 and 10 must be located in another chromosome, B; gene 4 must be located in a third chromosome, C. Gene 8 can not be in A but may be located in B, C or a fourth chromosome. With these assumptions all the data so far obtained fall into line and if these data are substantiated the other results predicted must hold if the chromosome hypothesis is correct. It must be noted that many of the cases cited here are not fully established on account of the small numbers, and furthermore there is the possibility that what is taken to be independent assortment may be crossing over of about 50 per cent.

⁵ This may also be a necessity on the reduplication hypothesis or may even be axiomatic and must hold for any and every hypothesis that might be put forth to account for factorial linkage.

Since the chromosome number is comparatively low ($1n=12$, Winkler, quoted after East, 1915) the tomato is rather favorable plant material in which to study linkage.

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